The Gyne of the Enigmatic Fungus-Farming Ant Species Mycetosoritis explicata

Jeffrey Sosa-Calvo, Seán G. Brady, and Ted R. Schultz*

 (JS-C, SGB, TRS) Department of Entomology, National Museum of Natural History, Smithsonian Institution, POB 37012, CE516, MRC 188, Washington, D.C. 20013-7012, USA
 (JS-C) Maryland Center for Systematic Entomology, Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD, 20742, USA

Abstract.—We describe for the first time the gyne of the Neotropical fungus-farming ant Mycetosoritis explicata, a species hitherto known from only two workers collected in Goias State, Brazil, in 1968. A redescription of the worker is presented. The likely non-monophyly of the genus Mycetosoritis and the possible position of the constituent species within the tribe Attini are discussed.

Key words.—Attini, Mycetosoritis, Myrmicinae, Neotropics, taxonomy

Mycetosoritis Wheeler (Formicidae: Myrmicinae: Attini) is perhaps the most enigmatic of all fungus-farming ant genera. This taxon was erected by Wheeler (1907) as a subgenus of Atta Fabricius to accommodate the species M. aspera (Mayr) and M. hartmanni (Wheeler), and was raised to genus status by Creighton (1950). Mycetosoritis currently comprises five species: M. aspera, M. clorindae (Kusnezov), M. explicata Kempf (all southern South American), M. hartmanni (southern United States), and M. vinsoni Mackay (Costa Rica and Nicaragua). Emery (1906), Wheeler (1907), and Creighton (1950) all agreed that Mycetosoritis species combine characters otherwise found exclusively in either Cyphomyrmex Mayr or Trachymyrmex Forel. As pointed out by Kempf (1968), "... it must be admitted that this group, as defined by Emery (1922), is highly heterogenic."

Emery (1921, 1922) and Creighton (1950) did their best to list the characters uniting the species of *Mycetosoritis*, including: frontal lobes expanded and overhanging the clypeus (shared with most *Cyphomyr*-

* Author for correspondence

mex); antennal scrobe complete (shared with the Cyphomyrmex strigatus species group; with C. longiscapus Weber, C. muelleri Schultz & Solomon, C. wheeleri Forel, and C. costatus Mann; and with some species of the *T. opulentus* group); and body hairs erect or curved, arising from tubercles at least on the gaster (shared with Trachymyrmex and Acromyrmex). The species M. hartmanni, M. vinsoni, and M. clorindae share with most Cyphomyrmex species an eroded sculpturing of the alitrunk and a generally smooth integument, whereas M. aspera and M. explicata share with many Trachymyrmex and Acromyrmex species a rougher integument punctuated by tubercules. For these and other reasons, we find it doubtful that the five species currently placed in the genus Mycetosoritis form a monophyletic group, except that M. hartmanni and M. vinsoni are clearly either sister species or conspecific. The polyphyly of Mycetosoritis is also supported by molecular phylogenetic data (Schultz and Brady 2008).

Mycetosoritis explicata, the focus of this paper, is exceedingly rare in collections, and its biology remains completely un-

known. This species was described by Kempf (1968) based on two worker specimens. Besides these, only four other worker specimens are known to exist in collections. Herein we describe and figure the heretofore unknown gyne of this species. We also provide information about and figures of the poorly known worker caste. We conclude with a discussion of morphological characters relating the five species of *Mycetosoritis* to other members of the Attini.

MATERIALS AND METHODS

Examination and measurement of specimens were completed at various magnifications using a Leica MZ16 light stereomicroscope and were recorded to the nearest 0.001 mm. Specimens were photographed using a JVC KY-F75U FireWire digital camera mounted on a Leica Z16 APO microscope with a Leica Motor-focus System attached to a Dell Optiplex GX620 computer, on which composite images were assembled using Auto-Montage Pro Version 5.03.0018 BETA software® (Synoptics Ltd.). Scanning Electron Micrographs (SEM) of uncoated specimens were taken using a Philips XL-30 ESEM with LaB6 under low vacuum conditions, gas pressure ranging between 0.7-0.9 Torr, and a backscatter detector. Images were cropped and enhanced using Photoshop CS2 Version 9.0.2® (Adobe Inc.).

SYSTEMATIC TREATMENT

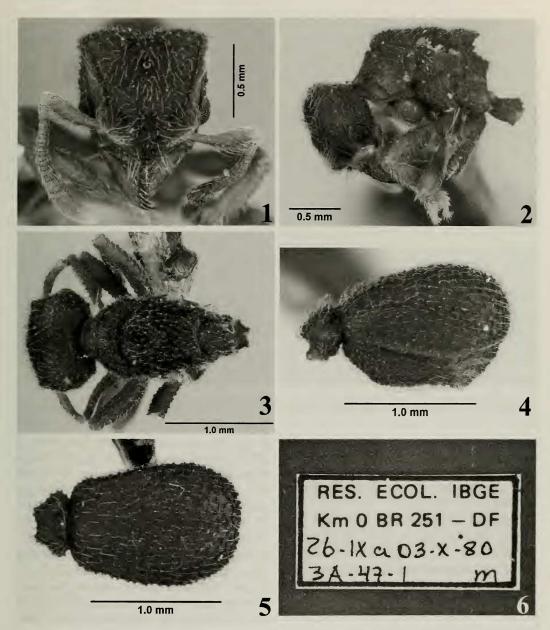
Description

Mycetosoritis explicata Kempf GYNE (Figs 1–7, 9, 10)

Label data: "Res. Ecol. IBGE; Km 0 BR 251 – DF; 26 ix a 03 x 80; 3A- 47- 1 m" (Referring to Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE), Distrito Federal - DF, Brasilia, Brazil.) Measurements (in mm): Head

Length = 0.94; Head Width (excluding eyes) = 0.93; Mandible Length = 0.63; Weber's Length = 1.49; Scape Length (excluding the antennal condyle) = 0.64; Hind Femur Length = 0.99; Greatest Diameter of Eye = 0.23. Deposition: Reserva Ecológica IBGE, Brasilia, Brazil.

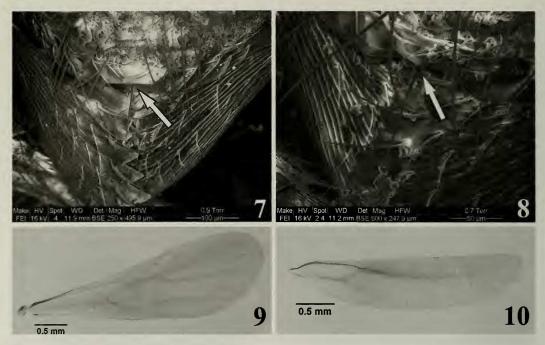
Head.—In full-face view, head nearly as broad as long, posterior margin angulate at corners and impressed medially. Mandibles longitudinally striate and bearing 8 teeth, gradually increasing in size from the base. Clypeal apron broadly convex, the convexity interrupted medially by a conspicuous emarginate notch. A median seta (~0.16 mm in length) originates on the anteriormost edge of the clypeal apron, does not at all overlap the body of the clypeus, and extends across approximately one-fourth the length of the mandibles. Three pairs of lateral setae, long and simple and curved mesad, also originate on the clypeal apron. A pair of setal brushes, originating on clypeus below the frontal lobes, each consist of approximately 7-9 long setae and extend to one-half the length of the mandibles. Frontoclypeal teeth vestigial. Frontal lobes semicircular and greatly expanded, attaining the width of the head below the eyes (0.70 mm). Borders of the frontal lobes denticulate, imparting a serrated appearance. Frontal carinae produced into a denticulate lamina. Supraocular tubercle absent. Frontal carinae extending to posterior margin, there joining the subocular carinae to form a complete antennal scrobe. Antennal scape short, not exceeding the length of the scrobe. Anterior edge of the antennal scape denticulate, with subdecumbent long hairs that project toward the apex; posterior edge lacking denticles and bearing appressed hairs. Nuchal carina present and complete. Antennal scape in full-face view narrow in basal one-third, much broader in apical two-thirds, although slightly narrower at apex. Antenna 11-segmented, final segment approximately one-third the length of the flagellum. Eye with 14



Figs 1–6. Gyne of *Mycetosoritis explicata*. 1, head, full-face view. 2, head, mesosoma, and petiole, lateral view. 3, head, mesosoma, and petiole, dorsal view. 4, postpetiole and gaster, lateral view. 5, postpetiole and gaster, dorsal view. 6, specimen label.

ommatidia across its greatest diameter. Three small ocelli present, distance between the posterior pair 1.3 times the maximum diameter of the eye.

Mesosoma.—Pronotum with a pair of short lateral tubercles connected by a conspicuous posterior pronotal carina, most easily seen in frontodorsal view. Inferior corner of pronotum forming an obtuse angle, lacking a tooth or spine. Scutum without notable large divisions. Parapsidal lines distinct and raised, extending approximately half the length of the scutum. Axillae narrowly contiguous,



Figs 7-8. Scanning electron micrographs of the clypeal apron, showing the origin of the unpaired median seta, dorsal view. 7, gyne of Mycetosoritis explicata. 8, worker (paratype) of M. explicata.

Figs 9-10. Wings of the gyne of Mycetosoritis explicata. 9, fore wing. 10, hind wing.

separated from scutellum by a broad, deep furrow. Scutellar process with a pair of posterior rounded teeth. Propodeal teeth short and obtuse. Propodeal spiracles small and directed posterad. Outer surface of tibia armed with a row of denticles not found on inner margin.

Metasoma.—Petiolar node approximately as long as broad, with a pair of tubercles on the posterior of the dorsum and several lateral denticles. Postpetiole wider than long; dorsum slightly concave, with lateral carinae; sides bearing several denticles; posterior margin vestigially emarginate. First gastral tergite (abdominal tergite IV) with pair of lateral carinae in anterior twothirds; dorsum with small, pimple-like, piligerous tubercles which are connected to each other by rugae, forming an areolate surface sculpture. First gastral tergite longer than sternite, dorsally overhanging remaining segments. Terminus directed away and downward from longitudinal axis of body.

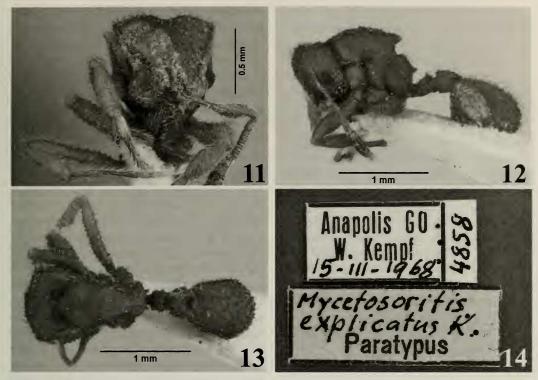
Wings.—Transparent, with minute hairs. Fore wing (length = 3.71 mm) with five

closed cells (terms follow Goulet and Huber 1993): costal (C), radial (R), cubital (Cu), first radial 1 (1R1), and first radial 2 (2R1); pterostigma small and pale (same color as veins); junction of cross-vein 1Cu-a and anal vein rounded, anal vein not extending past junction. Venation of hind wing (length= 3.08 mm) extremely reduced; seven hamuli on anterior margin.

Body color dark reddish-brown. Sculpture scabrous and areolate, particularly on scapes, legs, and gaster, due to the presence of scattered, pointed, piligerous pimples connected by irregular rugae. Hairs long, flexuous, and mostly strongly recurved, especially on clypeus, scapes, and gaster.

WORKER (Figs 8, 11–14)

Label data: "PARATYPE, BRAZIL, GO, Anapolis, W. Kempf, 15 iii 1968; 4858." This is the paratype specimen described in Kempf (1968) as "taken in the savannah



Figs 11–14. Paratype worker of *Mycetosoritis explicata*. 11, head, in full-face view. 12, body, lateral view. 13, body, dorsal view. 14, specimen labels.

south of the city of Anápolis, near Km 46 of the Goiânia-Brasília highway, Goiás State, Brazil, on March 15, 1968, W. W. Kempf leg. (WWK 4858)."

Measurements (in mm): Head Length= 0.80; Head Width (excluding eyes)= 0.80; Mandible Length= 0.48; Weber's Length= 1.20; Scape Length (excluding the antennal condyle)= 0.58; Hind Femur Length= 0.92; greatest diameter of eye= 0.16. Deposition: Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo, Brazil.

Non-Paratypic material examined

1 worker, BOLIVIA, Santa Cruz, Perforación, 68 Km ESE Charagua, 11 xii 1993, 470 m, 19°55′ S 62°34′ W, ground forager, tropical dry forest, collector *P. Ward.* (PSW 12335-5). Deposition: Museum of Comparative Zoology (MCZC), Cambridge, Massachusetts, U.S.A. 1 worker, BRAZIL, Brasilia, DF, UnB [Universidade de Brasilia] Campus, 28 viii 1976, in Cerrado habitat, collector *J.L.M. Diniz.* (JLMD 1102).

Deposition: J. Diniz personal collection. 1 worker, PARAGUAY, Boquerón, Enciso, 3–6 xi 2001, 21°12′ S 61°40′ W, dry Chaco, sifted litter, collectors *M. LePonce* and *T. Delsinne* (#4075-41). Deposition: Alex L. Wild personal collection (ALWC). Specimen image examined at: http://www.antweb.org/specimen.do?name=casent0173987&shot=p&project=worldants

Characters and states similar to those of the gyne with the proper allowances for caste. Here we supplement the description of Kempf (1968).

Head.—In full-face view, head as broad as long. Mandibles triangular, inner margin with 8 teeth gradually increasing in size towards the apex. Eye with 10 ommatidia in the longest row. Median unpaired clypeal setae 0.09 mm long, originating on anteriormost edge of clypeus, a pair of lateral clypeal brushes consisting of 4–5 hairs each. Preocular carinae raised and extending backwards joining the frontal carinae at the occipital margin, forming a

complete antennal scrobe. Frontal lobes greatly expanded (0.59 mm). Nuchal carina present and complete. Anterior edge of the antennal scape denticulate, with subdecumbent long hairs that project toward the apex; posterior edge lacking denticles and bearing appressed hairs.

Mesosoma.—Dorsum of pronotum flat and with eroded sculpture or with some very small tubercles that bear some decumbent or subdecumbent hairs. Lateral margins of pronotum with a denticulate carinae. Lateral pronotal spine triangular and large. Lateral mesonotal tubercles large, triangular, and keeled. Posterior mesonotal lobes carinate. Dorsum of promesonotum forming a shield, carinate on all sides, separated from lateral portions of the promesonotum by abrupt right angles, and, posteriorly, overhanging and elevated above the propodeum. Basal lateral face of propodeum with carinules that end in small tubercles.

Metasoma.—Petiolar node approximately as long as broad, with a pair of dorsal bifid teeth. Postpetiole wider than long; sides bearing several denticles of similar length (differing from Kempf's [1968] description "... with a larger spine projecting from the middle of each side"); posterior margin vestigially emarginate. First gastral tergite (abdominal tergite IV) oblong, ovate, with pair of lateral carinae in anterior twothirds; dorsum with small, pimple-like, piligerous tubercles which are connected to each other by weak but conspicuous rugae, forming an areolate surface sculpture. First gastral tergite longer than sternite, dorsally overhanging remaining segments. Terminus as in the gyne.

Body color ferrugineous; gaster appears to be the same color (*contra* description in Kempf 1968). Color lighter than that of queen.

DISCUSSION

The gyne and worker of *M. explicata* are clearly associated with each other by several compelling characters: a distinctive

microsculpture; the apical segment of the antenna large, as long as one-third the length of the flagellum; the frontoclypeal teeth either vestigial (gyne) or completely absent (worker); clypeal setal brushes present (consisting of 7-9 long setae in gyne or 4-5 long setae in worker); the anterior edge of the antennal scape denticulate, with subdecumbent long hairs that project toward the apex, the posterior edge lacking denticles and bearing appressed hairs; long golden hairs present on clypeus, scapes, and gaster; inferior angle of pronotum obtusely angulate; mandibles longitudinally striate and bearing 8 teeth; and outer surface of tibia armed with a row of denticles not found on inner margin. The gyne and worker differ in that the teeth on the posterior face of propodeum are short and tuberculate in the gyne, while more tooth-like in the worker; worker with a pair of bifid teeth on the dorsum of the petiolar node, whereas gyne with a pair of tubercles on the dorsum of disc of petiole; and color, being ferruginous in the worker and dark reddish-brown in gyne.

Since the creation of Mycetosoritis by Wheeler (1907), researchers have doubted the monophyly of Mycetosoritis and have disagreed about the phylogenetic positions of its constituent species. Wheeler (1907) stated that Mycetosoritis hartmanni "may be regarded either as a degenerate and simplified Trachymyrmex or as an aberrant Cyphomyrmex." Forel (1911) and Weber (1972) regarded Mycetosoritis as a primitive attine, transitional between Cyphomyrmex (considered by them to be the most primitive attine genus) and the remaining Attini. Forel (1912) placed the genus in one of two parallel attine "phyletic series," again as transitional between Cyphomyrmex and Mycocepurus Forel. Alternatively, Emery (1912), Wilson (1971), and Hölldobler and Wilson (1990) placed Mycetosoritis as closely related to the higher attines. The phylogeny of Schultz and Meier (1995) placed M. hartmanni as the sister group of the combined Cyphomyrmex and the higher

attines. Kempf (1964, 1968) compared *M. aspera, M. clorindae*, and *M. explicata* to members of the *Cyphomyrmex strigatus* group, based on the similar forms of the antennal scrobe, and implied that they may not be closely related to *M. hartmanni*. Of the genus *Mycetosoritis*, he states that "it must be admitted that this group, as defined by Emery (1922), is highly heterogenic. The type species *hartmanni* from Texas is quite distinct from the two South American species *aspera* and *clorindae* ..."

Our opinion is that M. aspera and M. explicata are more closely related to the higher attines (defined to include Mycetagroicus, Trachymyrmex, Sericomyrmex Mayr, Acromyrmex Mayr, and Atta), whereas M. clorindae, M. hartmanni, and M. vinsoni are much more distantly related to the higher attines. Based on molecular phylogenetic analyses (Schultz and Brady 2008), the latter two species are the extant representatives of a lineage that diverged early in the evolution of the Neoattini, prior to the origin of the common ancestor of Cyphomyrmex and the higher Attini. One morphological character that may link M. aspera and M. explicata to the higher attines is the reticulate sculpture, most notably on the gaster, shared with some Mycetagroicus Brandão & Mayhé-Nunes and some Trachymyrmex (e.g. T. opulentus) species. It is true, however, that the semicircular and greatly expanded frontal lobes constitute a character shared with most Cyphomyrmex species and that the complete antennal scrobe, formed by the frontal carinae extending to occipital corners and joining the subocular carinae, is a state shared with members of the Cyphomyrmex strigatus species group as well as with a subset of Trachymyrmex species, including those in the *T. opulentus* group. Obviously, the affinities of the five Mycetosoritis species remain enigmatic and will not be resolved until they are included in comprehensive morphological and molecular phylogenetic analyses. Such analyses, in turn, will only become possible when increased collecting corrects the exasperating rarity of specimens of M. aspera, M. explicata, and M. clorindae.

ACKNOWLEDGEMENTS

We thank the collection of the Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE), Jacques Delabie, and Roberto C.F. Brandão for loaning specimens; Eduardo Sanhudo and Jorge L.M. Diniz for useful information regarding the species; and Scott Whitaker (USNM) for assistance with the scanning electronic micrographs. This work was supported by National Science Foundation grants IRCEB DEB 0110073 to TRS and EF-0431330 to SGB and TRS. Additional funding was provided by the Ernst Mayr Travel Grant in Animal Systematics (Museum of Comparative Zoology) and the Jacob K. Goldhaber Travel Award (University of Maryland) to JSC. We are grateful to an anonymous reviewer for helpful comments on a previous version of the manuscript.

LITERATURE CITED

Creighton, W. S. 1950. The ants of North America. Bulletin of the Museum of Comparative Zoology of Harvard College 104: 1–585.

Emery, C. 1906. Studi sulle formiche della fauna Neotropica. *Bollettino della Societa Entomologica Italiana* 37: 107–194.

-----. 1912. Études sur les Myrmicinae. Annales de la Societe Entomologique de Belgique 56: 94–105.

fam. Myrmicinae. *Genera Insectorum* 174A: 1–94.

Forel, A. 1911. Ameisen des Herrn Prof. v. Ihering aus Brasilien (Sao Paulo usw.) nebst einigen anderen aus Südamerika und Afrika (Hym.). *Deutsche Entomologische Zeitschrift* 1911: 285–312.

——. 1912. Formicides Néotropiques. Part II. 3me sous-famille Myrmicinae Lep. (Attini, Dacetii, Cryptocerini). Memoires de la Societe Entomologique de Belgique 19: 179–209.

Goulet, H. and J. T. Huber. 1993. Hymenoptera of the World: An Identification Guide to Families. Research Branch, Agriculture Canada Publication 1894/E, Ottawa. 668 pp.

Hölldobler, B. and E. O. Wilson. 1990. *The Ants*. Belknap Press, Cambridge, Massachusetts. 732 pp.

Kempf, W. W. 1964. A revision of the Neotropical fungus-growing ants of the genus *Cyphomyrmex* Mayr. Part I. Group of strigatus Mayr (Hym., Formicidae). *Studia Entomologica* (N.S.) 7: 1–44.

— . 1968. Miscellaneous studies on Neotropical ants. IV. (Hymenoptera, Formicidae). Studia Entomologica (N.S.) 11: 369–415.

Mayr, G. L. 1887. Südamerikanische Formiciden. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 37: 511–632. Schultz, T. R. and R. Meier. 1995. A phylogenetic analysis of the fungus-growing ants (Hymenoptera: Formicidae: Attini) based on morphological characters of the larvae. *Systematic Entomology* 20: 337–370.

—— and S. G. Brady. 2008. Major evolutionary transitions in ant agriculture. *Proceedings of the National Academy of Sciences* 105: 5435–5440.

NOTE IN PROOF

After submitting the final version of this manuscript, the authors received from Thibaut Delsinne (Royal Belgian Institute of National Sciences) 3 workers and 1 dealate gyne of *M. explicata* collected in Paraguay, Boqueron. The label information for these specimens is as follows. 1 gyne, PARAGUAY, Boqueron, Enciso, 4–5 xi 2001, 21°20¹ S 61°66¹ W, 400–590m trail, collector M. Leponce (sample ID code 4057; sampling point: T 89.02.0 r1; Winkler 24h; specimen ID code 7688). 1 worker, PARA-

Weber, N. A. 1972. *Gardening ants, the attines*. American Philosophical Society, Philadelphia. 146 pp.

Wheeler, W. M. 1907. The fungus-growing ants of North America. *Bulletin of the American Museum of Natural History* 23: 669–807.

Wilson, E. O. 1971. *The insect societies*. Belknap Press, Harvard University, Cambridge, MA. 548 pp.

GUAY, Boqueron, Enciso, 1–2 x 2002, 21°211 S 61°661 W, collector T. Delsinne (sample ID code 9911; sampling point: Q 120.07.0 r1; Winkler 24h; specimen ID code 11539). 1 worker, PARAGUAY, Boqueron, Enciso, 4–5 xii 2001, 21°20¹ S 61°66¹ W, 800–990m trail, collector M. Leponce (sample ID code 4109; sampling point: T 90.14.0 r1; Winkler 24h; specimen ID code 22851). 1 worker PARAGUAY, Boqueron, Nueva Asuncion, 1–2 xi 2001, 20°70¹ S 61°93¹ W, 0–190m dunes, collector M. Leponce (sample ID code 3897; sampling point: T 85.02.0 r1; Winkler 24h; specimen ID code 22959).